THE EFFECT OF A CAVE ON BENTHIC INVERTEBRATE COMMUNITIES IN A SOUTH ISLAND STREAM

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ABSTRACT

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In its lower reaches Cave Stream flows through a pitch-black limestone tunnel. The effect of the cave on epilithic carbon and periphyton, invertebrate community structure (within and outside the cave), and drift was investigated. Stone surface organic layers were absent inside the cave but well developed outside. Invertebrate densities were considerably lower inside than outside the cave, although relative abundances of taxa were not markedly different. Drift rates and densities were higher at the inlet end of the cave than at the outlet indicating that the cave acted as a drift barrier to some invertebrate species, which may have been unable to survive on the low food resources inside. Despite a reduction in numbers of animals drifting into the downstream reaches of Cave Stream, community structure was not significantly different from that upstream of the cave. This points to the importance of oviposition and upstream migration as primary means of colonization for many taxa.

KEYWORDS: benthic invertebrates - periphyton depression - drift - cave - New Zealand streams.

INTRODUCTION

Instream primary production is the principal source of energy utilized by primary consumers in many streams (Minshall 1978). The impact of an increase in primary production as a result of forest removal has been documented in a number of studies (eg.,Hawkins *et al.* 1983, Murphy *et al.* 1981), but the effect of a decrease in primary production in predominantly autochthonous based stream communities has rarely been examined. One exception is the study by Towns (1981) of a northern New Zealand stream, in which artificial shading of a length of the stream bed caused changes in both the relative and absolute abundance of the major benthic invertebrate species. Similarly, McAuliffe (1984) observed reductions in the densities of some benthic invertebrate species in response to lower periphyton biomass, resulting in his study, from the grazing activities of caddisfly larvae.

Cave Stream, the site of the present study, passes through a 362 m long, limestone cave in its lower reaches. Above and below the cave the benthic invertebrate community appears to be reliant primarily on autochthonous (instream) sources of energy as the surrounding tussock grassland provides limited inputs of organic matter. The presence of a substantial, permanently dark segment of stream (the cave) offered an unusual opportunity to investigate the relationship between the occurrence of periphyton and the distribution of benthic invertebrates. It was hypothesized that periphyton production would be totally suppressed in the cave and that because of this lotic invertebrates would be unable to survive there for an extended period of time. It seemed likely therefore, that the cave might also act as a barrier to colonization of the lower reaches of the stream and result in the presence there of a fauna different from that above the cave.

The present study had three aims: 1) to investigate whether periphyton biomass was reduced in the cave, and if so, whether this precluded colonization by invertebrates; 2) to investigate whether the cave prevented colonization of downstream reaches of the stream by drift; and 3) to examine whether this in turn affected community composition in the downstream reaches.

STUDY AREA

Cave Stream is a second order tributary of Broken River that rises in the foothills of the Craigeburn Range, Canterbury. The stream is notable for the presence of a 362 m long limestone cave in its lower reaches. The present study was carried out from the confluence with Broken River to about 50 m upstream of the inlet end of the cave (latitude 43°12′ South; longitude 171°41′ East). In this area the stream has a mean width of 5.1 m, a mean depth of 27 cm and the bed consisted mainly of riffles and a few pools. Bottom substrate was either limestone bedrock (50%), small cobbles (10%) or a mixture of cobbles and boulders (40%). Stream water pH ranged from 7.1 to 8.1 over the course of the study and mean conductivity was 73 μS. cm^{-1} (at 25°C).

MATERIALS AND METHODS

STONE SURFACE LAYERS

Periphyton

Greywacke and limestone cobbles (mean diameter 6 cm) were collected from six sites along the stream, both inside and outside the cave, and returned to the laboratory in containers of stream water. Pigments were extracted with 90% acetone for 24 h in the dark at 5°C and concentrations of chlorophyll *a* and phaeopigment were measured using the method of Wetzel & Westlake (1969). Surface area of periphyton cover was estimated by weighing a traced cut-out of the stone surface area covered in periphyton and comparing it with the weight of a paper cut-out of known area. Light readings were taken where cobbles were collected, at 1000 h and 1600 h on the day of collection. They were measured with a photocell at the water surface.

Epilithic carbon

Greywacke cobbles (mean diameter 3 cm) were collected from three sites inside and outside the cave for organic carbon analysis of epilithon. Organic carbon was measured with the wet oxidation technique as modified by Collier (1987). Surface area of stones was estimated by weighing aluminium foil which was wrapped tightly around the stones and then comparing this with the weight of foil of known area.

Scanning electron microscopy

A Cambridge Stereoscan MK II scanning electron microscope (SEM) was used to make a qualitative comparison of stone surface layers from inside and outside the cave. Small stones (approximately 1.5 cm in diameter) were collected from three sites inside and outside the cave and fixed with 3% gluteraldehyde in phosphate buffer. They were dehydrated in an alcohol series as described by Rounick & Winterbourn (1983), dried in a vacuum desiccator and mounted on SEM stubs. After coating with 50 nm of carbon/gold palladium they were examined with the scanning electron microscope at magnifications up to 1000 times.

INVERTEBRATE DRIFT

Drift at the outlet and inlet ends of the cave was sampled twice with a triplicate drift sampler (Field-Dodgson 1985) positioned with the three net openings 7 cm apart and with the lower margins of the apertures 2-3 cm above the stream bed. On 19 February 1986, samples were taken every 4 hours starting at 1600 h for 32 hours. This period included a spate when discharge increased approximately 5 fold. On 27 February 1986, the sampler was set up at 1200 h and emptied at 2000 and 2400 hours and at 0800 and 1200 hours on the following day. Collections were preserved in 70% alcohol. Current velocity was measured in front of the samplers at the start and end of each 24 or 32 h period with a Pygmy Gurley Current Meter.

BENTHIC INVERTEBRATE COMMUNITIES

The benthic invertebrate fauna above the cave was compared with that below the cave on 6 February 1986 and 26 November 1988. On 16 and 27 February 1986, and 26 November 1988 the fauna at the outlet end of the cave was sampled at approximately 10 m intervals (where substrate was suitable) from its confluence with Broken River to the inlet end of the cave (this yielded 6, 5 and 10 samples from below the cave, in the transitional mouth region and inside the cave, respectively).

Samples were obtained with a 0.1 m^2 Surber sampler (250 μm mesh) except inside the cave at distances greater than 50 m from either end, where overhanging banks precluded the use of the sampler. Instead, a 0.1 m^2 quadrat was used there in conjunction with a 250 μm mesh kick net. Sampling was achieved by removing and hand scraping large stones and disturbing the remaining finer sediment to a depth of 5-10 cm. Samples were preserved and returned to the laboratory, sorted, and identified to the lowest possible taxonomic level.

Communities were compared in a number of ways: 1) Jaccard's coefficient (Jaccard 1902) was calculated to measure the proportion of species in common between two communities; 2) Cochran's Q-test (Cochran 1950, Pridmore 1985) was used to test whether species were independently distributed among samples from different sites; 3) A percentage similarity index (Whittaker 1952, Sanders 1960, Johnson & Brinkhurst 1971) was calculated, using mean density data for communities, to determine how similar the relative abundances of the component species were between communities (on a scale of increasing similarity from 0-100); 4) Spearman's rank correlation coefficients (Conover 1980) were calculated for common taxa (those with mean densities equal to or greater than 1 per 0.1 m^2) from mean abundance data to test species rankings between communities; 5) Mean densities of component species were compared with t-tests. Critical values for t-tests were calculated as described by Sokal & Rohlf (1981) because in most cases variances were not equal between communities.

RESULTS

STONE SURFACE LAYERS

Periphyton

Light intensity decreased exponentially from 2,300 lux at the mouth of the cave to 0 lux,28 m inside. Chlorophyll *a* (Fig. 1a) and phaeopigment (Fig. 1b) concentrations on both greywacke and limestone cobbles decreased with increasing distance inside the cave and were not detected 22 m within the cave. Pigment concentrations on both types of rock were significantly correlated with light intensity (r^2 = 0.76 - 0.92).

Epilithic carbon

Stones outside the cave had mean epilithic carbon concentrations of 3.3 μg cm^{-2} (S.E.=0.6) whereas no carbon was detected on stones further than 30 m inside the cave.

Scanning electron microscopy

Although the oxidation of stone surfaces did not reveal the presence of any epilithic carbon inside the cave, examination with the SEM revealed patches of fine fungal hyphae along with a very few diatom skeletons (Fig. 2a). Most of the stone surface was bare rock however, in contrast to the surfaces of stones from outside the cave which were densely covered with diatoms (Fig. 2b).

INVERTEBRATE DRIFT

Between 5 and 19 taxa were present in each

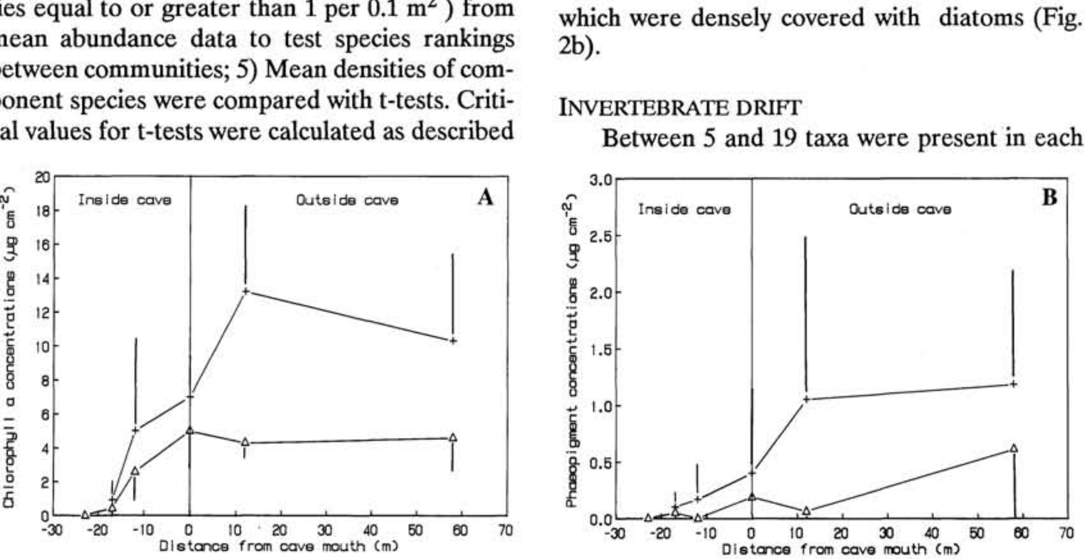

Figure 1. Mean chlorophyll *a* (A) and phaeopigment (B) concentrations (± S.E.) on limestone (+) and greywacke (▵) cobbles from sites along the outlet section of Cave Stream; 29 February 1986.

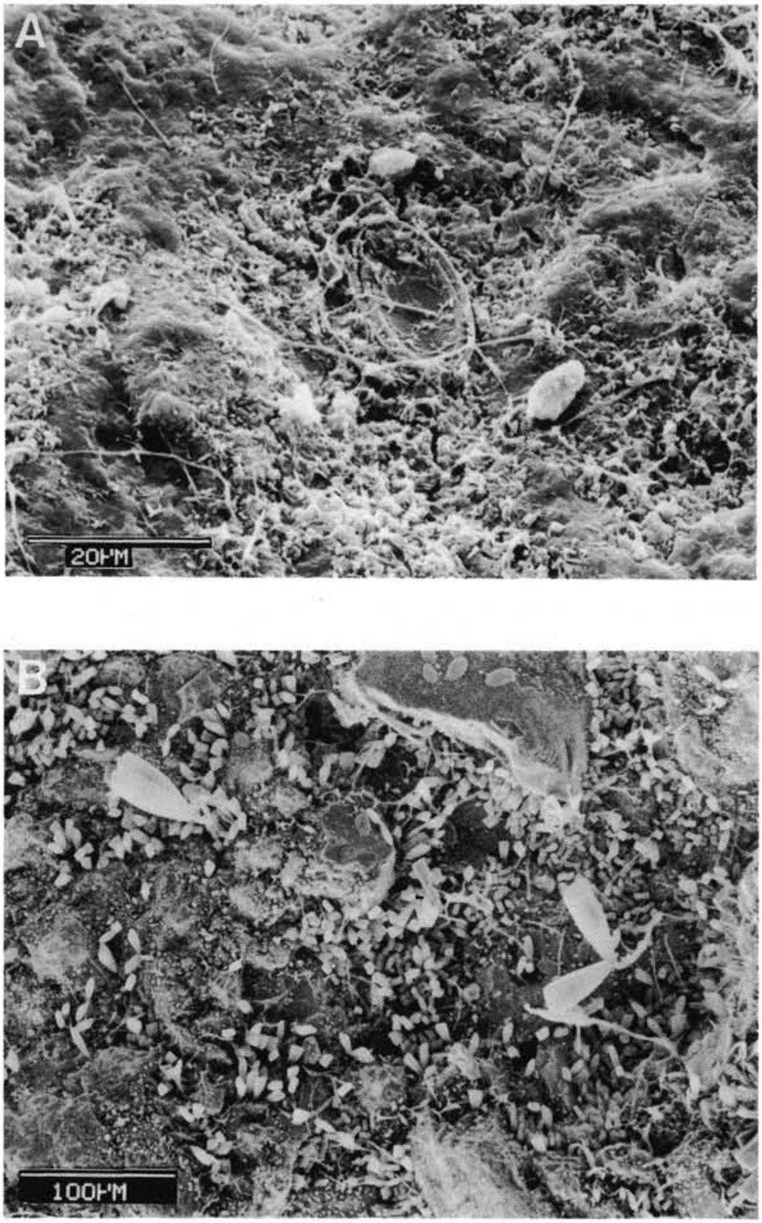

Figure 2. Scanning electron micrographs of stone surfaces from inside (A) and outside (B) the cave.

4-hour drift sample with *Deleatidium* sp., Chironomidae, *Olinga feredayi*, *Hydora* sp. and *Pycnocentrodes* sp. were most abundant. Mean numbers of the 8 most abundant species collected per drift interval on 19-20 and 27-28 February are plotted against time in Fig. 3. The number of animals collected on 19-20 February increased with time as a result of an increase in flow from 6-83 cm s^{-1} at the outlet sampling site and from 27-68 cm s^{-1} at the inlet site.

Analysis of variance (Table 1) indicated that numbers of drifting *Hydora* larvae and hydrobi-

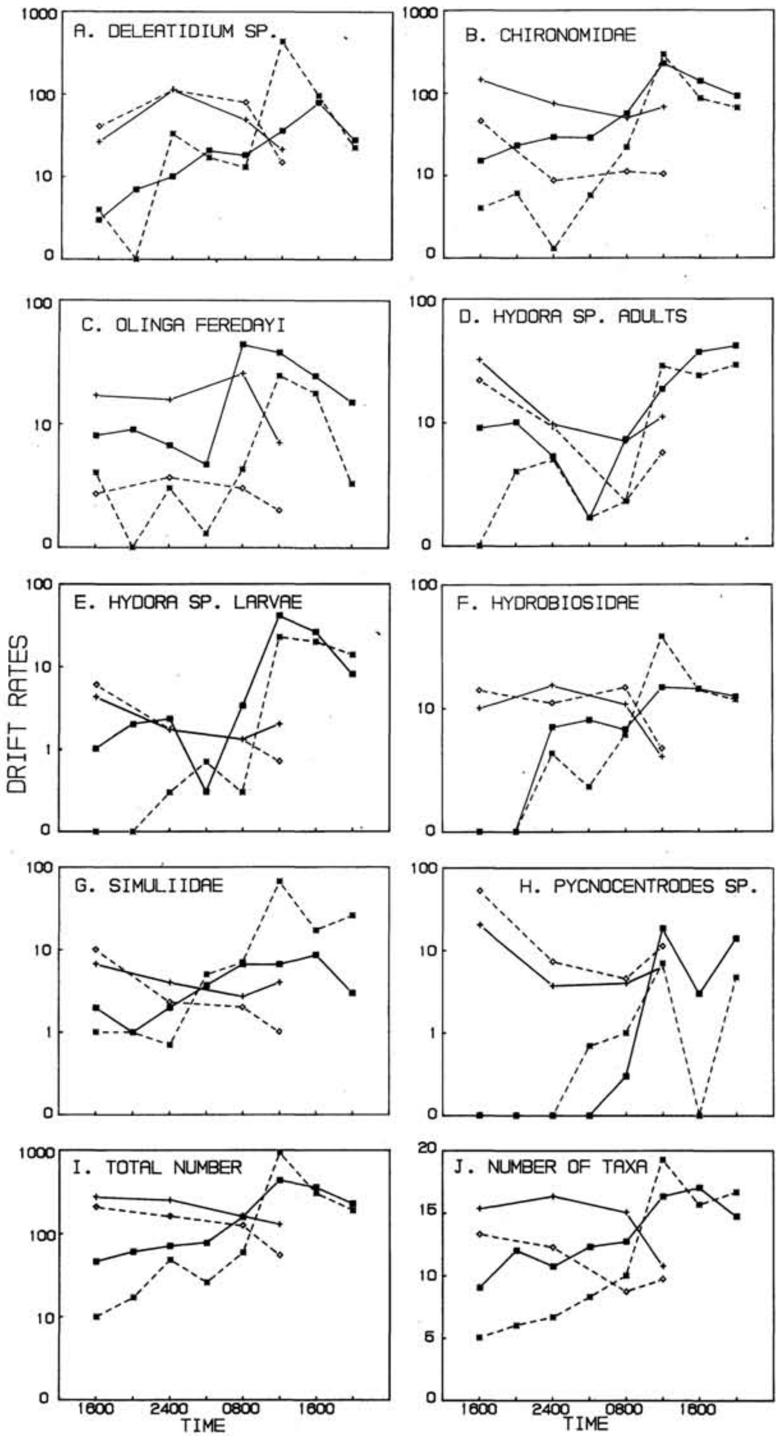

Figure 3. Mean numbers of invertebrates collected per sampling period in triplicate drift samples at the inlet (—) and outlet (- - -) ends of the cave between 1200 h on 19 February and 1600 h on 20 February 1986 (◇ & +) and between 1200 h on 27 February and 1200 h on 28 February 1986 (* & ▪). Sunset was at 2100 h and sunrise at 0700 h.

	19-20 FEBRUARY				27-28 FEBRUARY			
TAXON	*F*	*df*	*P*		*F*	*df*	*P*	
Deleatidium sp.	9.38	1,35	0.005	out>in	1.17	1,23	0.295	n.s.
Chironomidae	109.05	1,35	0.000	out<in	90.76	1,23	0.000	out<in
Olinga feredayi	68.68	1,35	0.000	out<in	66.25	1,23	0.000	out<in
Hydora sp. adults	1.84	1,35	0.188	n.s.	4.80	1,23	0.044	out<in
Hydora sp. larvae	1.74	1,35	0.200	n.s.	0.08	1,23	0.786	n.s.
Hydrobiosidae	1.24	1,35	0.276	n.s.	0.14	1,23	0.718	n.s.
Simuliidae	15.51	1,35	0.001	out>in	3.86	1,23	0.067	n.s.
Pycnocentrodes sp	6.72	1,35	0.016	out<in	9.26	1,23	0.008	out>in
Total number	7.70	1,35	0.011	out<in	37.09	1,23	0.000	out<in
Number of taxa	12.29	1,35	0.002	out<in	19.89	1,23	0.000	out<in

Table 1. Analysis of variance testing the null hypothesis that the number of individuals per unit time in the inlet and outlet drift collected on 19-20 and 27-28 February 1986 were similar. Analysis was carried out on $\ln(x+1)$ transformed data.

osid larvae were not significantly different ($P>0.05$) at that inlet and outlet on either occasion, but numbers of larval Chironomidae, *Olinga feredayi,* taxa and total invertebrates were all significantly higher ($P<0.05$) in inlet drift. *Hydora* adults had significantly lower numbers in the outlet drift, but only on 27-28 February ($P=0.044$). Significantly more *Deleatidium* and *Austrosimulium tillyardianum* larvae were taken in the outlet drift samples on 19-20 February when flow increased as a result of a spate. Results obtained for *Pycnocentrodes* sp. were inconsistent, with significantly higher numbers in inlet drift on 19-20 February and higher numbers in outlet drift on 27-28 February.

Analysis of variance on drift density data produced similar results to that for drift rates, the hydrobiosids being the only group to show a major difference, with drift densities significantly higher at the inlet on both occasions.

BENTHIC COMMUNITIES INSIDE AND OUTSIDE THE CAVE

Samples of invertebrates collected on 16 and 27 February 1986 were allocated to one of three groups: 1) outside the cave at the outlet end; 2) inside the mouth of the cave where light still penetrated (a distance of about 28 m); and 3) inside the cave where light was absent. Mean densities of invertebrates in each of these groups are given in Table 2 and mean densities of those collected outside and inside the cave (excluding group 2) on 26 November 1988 are shown in Table 3.

On both dates, densities of invertebrates inside the cave were consistently lower than outside. Almost all the more abundant animals (i.e. those with mean densities greater then 1 per 0.1 m^2) had significantly lower densities inside the cave, although two exceptions were *Austrosimulium tillyardianum* and *Aoteapsyche colonica*. They had similar densities inside and outside the cave in February, but were more abundant outside in November when densities were lower.

In February, 19 of the 36 collected species were found both inside and outside the cave, while 18 of the species were found inside and at the mouth of the cave. However, of the 23 species collected in the cave only 3, *Hydrobiosella stenocerca,* Helodid sp.B and a species of Hydraenidae, (represented by 3 individuals) were found exclusively inside the cave. Of the 34 species collected in November, only 12 and 11 were common to both the inside and outside, at the outlet and inlet ends respectively. All of the 12 species collected in the cave were also found outside. Cochran's Q values were significant in all cases indicating that assemblages compared on the basis of presence and absence of taxa were different inside and outside the cave. However, percentage similarity of communities inside and outside the cave was high on both occasions (range from 73% to 88% for all comparisons). Relative abundances of common taxa differed

	OUTLET		MOUTH		INSIDE				
SPECIES	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	$T_{(o-m)}$	$T_{(o-i)}$	$T_{(m-i)}$
Neppia montana	1.0	0.535	4.0	1.265	0.3	0.213	-1.989	1.216	2.884*
Oligochaeta	0.3	0.286	0.2	0.200	0.0	0.000	0.591	1.000	1.000
Archichauliodes diversus	4.0	1.309	0.6	0.400	0.6	0.400	2.484*	2.484*	0.000
Coloburiscus humeralis	0.4	0.202	1.0	0.548	0.5	0.307	-0.979	-0.432	1.494
Nesameletus sp.	3.6	1.660	2.6	1.208	0.5	0.307	0.196	1.820	1.684
Deleatidium sp.	189.7	21.881	192.4	39.438	60.0	8.610	-0.002	5.516*	3.280*
Zelandoperla decorata	0.7	0.184	0.0	0.000	0.0	0.000	3.873*	3.873*	--
Zelandobius furcillatus	2.3	0.918	0.6	0.600	0.2	0.200	1.153	2.219	0.633
Zelandobius n. sp.	0.3	0.184	0.0	0.000	0.0	0.000	1.549	1.549	--
Hydraenidae	0.0	0.000	0.0	0.000	0.1	0.100	--	-1.000	-1.000
Helodid sp.B	0.0	0.000	0.0	0.000	0.1	0.100	--	-1.000	-1.000
Hydora sp. larvae	30.1	9.359	1.6	1.122	0.3	0.153	3.028*	3.188*	1.148
Hydora sp. adult	1.9	1.223	0.8	0.583	0.3	0.213	0.443	1.254	0.805
Eriopterini sp.	0.1	0.143	0.0	0.000	0.0	0.000	1.000	1.000	--
Austrosimulium tillarydianum	3.1	1.580	6.4	4.844	6.3	2.561	-0.639	-0.281	0.004
Maoridiamesa harrisi	3.9	1.184	0.0	0.000	0.0	0.000	3.258*	3.258*	--
Orthocladiinae sp. type A	3.6	1.824	0.2	0.200	0.1	0.100	1.838	1.901	2.549*
Orthocladiinae spp. type B	21.7	10.237	2.6	1.122	0.2	0.133	1.856	2.101	2.123
Chironominae sp.	0.3	0.286	0.0	0.000	0.0	0.000	1.000	1.000	--
Empididae	0.1	0.143	0.2	0.200	0.0	0.000	-1.006	1.000	1.000
Limnophora sp.	0.6	0.429	0.4	0.245	0.0	0.000	0.561	1.333	1.633
Hydrobiosella stenocerca	0.0	0.000	0.0	0.000	0.1	0.100	--	-1.000	-1.000
Helicopsyche sp.	0.1	0.143	0.0	0.000	0.1	0.100	1.000	1.507	-1.000
Aoteapsyche colonica	2.1	0.508	1.4	0.927	1.6	0.618	0.772	0.741	-0.168
Hydrobiosis parumbripennis	1.3	0.421	0.2	0.200	0.1	0.100	2.331	2.743*	2.549*
H. clavigera	0.9	0.553	1.0	0.447	0.0	0.000	-0.247	1.549	2.236
H. indent.	0.1	0.143	0.2	0.200	0.0	0.000	-1.006	1.000	1.000
Psilochorema sp.	2.7	0.918	1.0	0.632	0.5	0.224	1.151	2.343	0.745
Costachorema xanthoptera	0.0	0.000	0.2	0.200	0.0	0.000	-1.000	--	1.000
early instar Hydrobiosidae	2.0	0.756	0.2	0.200	0.6	0.306	2.302	1.717	-1.884
Oxyethira albiceps	1.0	0.378	0.0	0.000	0.0	0.000	2.646*	2.646*	--
Hudsonema amabilis	0.3	0.184	0.0	0.000	0.1	0.100	1.549	4.926*	-1.000
Pycnocentrodes sp.	18.6	5.241	10.0	3.362	1.7	1.055	0.181	3.156*	2.356
Beraeoptera roria	0.0	0.000	0.2	0.200	0.4	0.267	-1.000	-1.500	-1.204
Conuxia gunni	0.0	0.000	0.2	0.200	0.0	0.000	-1.000	--	1.000
Olinga feredayi	16.9	2.899	28.6	4.611	3.4	0.909	-0.440	4.430*	5.362*
Chironomidae pupae	2.7	1.085	1.2	0.490	0.0	0.000	1.272	2.502*	2.450

Table 2. Mean densities (and one standard error) of benthic invertebrates collected in 0.1 m^2 Surber samples on the 16 and 27 February 1986 at the outlet end of the cave, in the mouth of the cave where light still penetrated and inside the cave. Values of T are also shown and significance values ($P<0.05$) indicated as (*).

outside and inside the cave in February ($r_s=0.39$, $df=19$, $P>0.05$), whereas in November Spearman's rank correlations indicated they were similar (both outlet and inlet ends) ($r_s=0.69$ and 0.70 for correlations between cave fauna and outlet and inlet end faunas respectively, $df=16$, $P<0.05$).

The fauna within the mouth of the cave

	OUTLET		CAVE		INLET				
SPECIES	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.	$T_{(o-i)}$	$T_{(o-c)}$	$T_{(i-c)}$
Neppia montana	0.0	0.000	0.0	0.000	1.0	0.408	-2.450	--	2.450
Potamopygrus antipodarum	0.0	0.000	0.0	0.000	0.3	0.250	-1.000	--	1.000
Oligochaeta	1.3	0.479	0.1	0.111	0.5	0.500	1.565	2.318	0.759
Archichauliodes diversus	1.3	0.750	0.1	0.111	3.5	0.645	-2.298	1.502	5.174*
Coloburiscus humeralis	0.5	0.289	0.0	0.000	2.0	1.225	-1.192	1.732	1.633
Nesameletus sp.	1.5	0.500	0.0	0.000	1.3	0.479	0.522	3.000	2.611
Deleatidium sp.	269.8	33.631	30.9	7.152	233.8	57.620	0.008	6.947*	3.494*
Zelandoperla decorata	0.3	0.250	0.0	0.000	0.0	0.000	1.000	1.000	--
Zelandobius furcillatus	0.8	0.479	0.0	0.000	0.3	0.250	1.714	1.567	1.000
Hydraenidae	0.3	0.250	0.0	0.000	0.0	0.000	1.000	1.000	--
Hydora sp. larvae	32.8	8.420	0.7	0.373	20.8	10.258	0.068	3.807*	1.957
Hydora sp. adult	0.8	0.250	0.0	0.000	0.5	0.289	1.714	3.000	1.732
Aphrophila neozelandica	0.0	0.000	0.0	0.000	0.3	0.250	-1.000	--	1.000
Eriopterini sp.	0.0	0.000	0.0	0.000	0.3	0.250	-1.000	--	1.000
Austrosimulium tillyardianum	24.3	13.047	0.1	0.111	16.5	6.238	0.037	1.850	2.627
Podonominae	4.3	3.326	0.4	0.338	3.3	1.315	0.078	1.138	2.066
Maoridiamesa harrisi	7.5	5.867	0.2	0.147	6.0	2.582	0.037	1.240	2.234
Orthocladiinae sp. type B	0.8	0.479	0.0	0.000	0.0	0.000	1.567	1.567	--
Orthocladiinae spp. type A	9.3	3.966	0.0	0.000	4.3	1.109	1.214	2.333	3.833*
Chironominae sp.	0.0	0.000	0.0	0.000	0.5	0.500	-1.000	--	1.000
Macropelopiini	0.5	0.289	0.0	0.000	0.0	0.000	1.732	1.732	--
Empididae	0.8	0.479	0.1	0.111	0.0	0.000	1.567	1.300	-1.000
Polyplectropus puerilis	3.8	2.175	0.0	0.000	0.3	0.250	1.599	1.724	1.000
Helicopsyche sp.	0.3	0.250	0.0	0.000	0.3	0.250	0.000	1.000	1.000
Aoteapsyche colonica	4.3	1.652	0.1	0.111	5.5	1.708	-0.221	2.500	3.149
Hydrobiosis parumbripennis	0.0	0.000	0.0	0.000	0.3	0.250	-1.000	--	1.000
Psilochorema sp.	0.3	0.250	0.0	0.000	0.8	0.479	-1.714	1.000	1.567
Early instar Hydrobiosidae	1.0	1.000	0.0	0.000	0.3	0.250	0.728	1.000	1.000
Pycnocentrodes sp.	37.3	5.422	0.3	0.236	16.5	5.172	0.370	6.803*	3.122
Beraeoptera roria	5.5	2.327	0.0	0.000	8.0	1.080	-0.380	2.363	7.407*
Olinga feredayi	0.8	0.479	0.1	0.111	2.5	0.289	-5.600*	1.300	38.525*
Acarina indet. A	0.3	0.250	0.0	0.000	0.5	0.500	-0.800	1.000	1.000
Acarina indet. B	15.3	1.887	1.9	0.588	14.3	3.637	0.060	6.759*	3.355*
Acarina indet. C	1.0	0.707	0.0	0.000	1.0	1.000	0.000	1.414	1.000
Hydrobiosidae pupae	1.0	0.707	0.0	0.000	0.5	0.289	0.857	1.414	1.732
Simuliidae pupae	0.3	0.250	0.0	0.000	0.0	0.000	1.000	1.000	--
Chironomidae pupae	3.8	2.496	0.0	0.000	2.5	1.041	0.171	1.503	2.402

Table 3. Mean densities (and one standard error) of benthic invertebrates collected in 0.1 m^2 Surber samples inside, and at the inlet and outlet ends of the cave on the 26 November 1988. T-test values are also shown and significant values ($P < 0.05$) indicated by (*).

where light still penetrated was also different from that outside in a number of respects. Thus larvae of *Archichauliodes diversus, Zelandoperla decorata*, *Hydora* sp., *Maoridiamesa harrisi* and *Oxyethira albiceps* all had significantly lower densities in the mouth of the cave. A significant value for Cochran's Q was also obtained ($Q = 90.3$, $df = 11$, $P < 0.05$) indicating the presence of different assemblages in the two sections of stream, even though, they shared 22 of 33 col-

SPECIES	INLET MEAN	S.E.	OUTLET MEAN	S.E.	T
Nematomorpha	0.0	0.000	0.3	0.250	-1.000
Neppia montana	3.5	0.500	0.3	0.250	13.867*
Archichauliodes diversus	4.0	2.000	2.3	0.250	0.868
Coloburiscus humeralis	0.0	0.000	0.5	0.500	-1.000
Nesameletus sp.	5.0	0.000	1.5	0.645	5.422 *
Deleatidium sp.	52.5	12.500	61.5	19.994	-0.009
Hydora sp. larvae	5.0	1.000	4.3	3.324	0.030
Hydora sp. adult	1.5	0.500	2.5	1.190	-0.305
Eriopterini sp.	0.0	0.000	0.5	0.500	-1.000
Austrosimulium tillyardianum	2.0	0.000	2.3	1.601	-0.156
Maoridiamesa harrisi	0.5	0.500	0.5	0.500	0.000
Tanypodinae	1.0	0.000	0.3	0.250	3.000
Orthocladiinae sp.	0.5	0.500	0.0	0.000	1.000
Polyplectropus puerilis	0.0	0.000	0.3	0.250	-1.000
Aoteapsyche colonica	0.0	0.000	0.3	0.250	-1.000
Hydrobiosis parumbripennis	1.5	0.500	0.3	0.250	5.333*
Psilochorema sp.	0.5	0.500	0.0	0.000	1.000
early instar Hydrobiosidae	1.0	0.000	0.3	0.250	3.000
Oxyethira albiceps	0.5	0.500	0.0	0.000	1.000
Pycnocentrodes sp.	0.0	0.000	0.5	0.500	-1.000
Olinga feredayi	8.0	6.000	5.3	2.016	0.122
Chironomidae pupae	0.5	0.500	0.0	0.000	1.000
Hydrobiosidae pupae	0.0	0.000	0.3	0.250	-1.000

Table 4. Mean densities (and one standard error) of benthic invertebrates collected in 0.1 m^2 Surber samples at the inlet and outlet ends of the cave on 6 February 1986 with t-test values used to compare densities (significance is accepted only at the 5% level indicated by *).

lected species. Percentage similarity of the communities was also high (PSc=76.4) but rank abundances were not significantly correlated (r_s=0.44, df=19, P>0.05).

Benthic communities at the inlet and outlet

Numbers of invertebrates collected outside the cave on 6 February 1986 and 26 November 1988 are shown in Tables 3 and 4, respectively. Species composition was similar above and below the cave. In February, 12 of the 21 collected species were found at both sites, whereas in November 23 of the 34 collected species were present at the inlet and outlet sites. In February the species were not independently distributed in all the samples however (Q=44.8, df=5, P<0.05) and distinct inlet and outlet communities could be identified. The November samples were independently distributed (Q=10.9, df=7, P>0.1) with no difference between the two communities. Percentage similarity of the communities was high with index values of 82% and 91% respectively, and Spearman rank correlations of the common taxa were also significant on both occasions (February r_s=0.76, df=10, P<0.05 ; November r_s=0.90, df=16, P<0.05).

When the mean densities of individual species were compared separately, little difference was found between the two sampling sites. In February, only *Neppia montana*, *Nesameletus* sp. and *Hydrobiosis parumbripennis* had significantly different densities at the inlet and outlet sites (with higher densities at the inlet end), and in November, *Olinga feredayi* was the only one of 34 collected species whose density differed significantly between the two ends of the cave (also with a higher density at the inlet end).

DISCUSSION

Forty seven species were collected from Cave Stream. *Deleatidium* sp. was numerically dominant inside and outside the cave and *Pycnocentrodes* sp., *Olinga feredayi*, *Austrosimulium tillyardianum* and *Hydora* sp. were also common.

Epilithic periphyton was absent inside the cave and stone surface organic layers were poorly developed, consisting of only sparse fungal hyphae; periphyton was abundant outside the cave however. Benthic material suitable as food for benthic invertebrates, apart from a very small amount of allochthonous particulate organic matter was therefore absent inside the cave. Probably as a consequence of this, densities of invertebrates were lower inside the cave, although the relative abundance of most animals was unaffected (i.e. most taxa were affected equally by low food available). Exceptions to this were the larvae of *Aoteapsyche colonica* and *Austrosimulium tillyardianum* which feed on suspended fine particulate matter (and drifting invertebrates in the case of *Aoteapsyche*), and were unaffected by the paucity of epilithon.

This "community" response parallels that observed by Towns (1981) who artificially shaded a section of stream with a canopy and found that numbers of *Hydrobiosis parumbripennis*, *Oxyethira albiceps*, *Pycnocentrodes* sp. and several species of Chironomidae including *Maoridiamesa harrisi* were reduced in the shaded portion. Total numbers of invertebrates were unaffected in his study however, as densities of oligochaetes, simuliids, and *Aoteapsyche colonica* increased beneath the canopy. This contrasts with the condition observed in Cave Stream and can probably be attributed to the smaller size of his artificial "cave" (length 8 m) and the presence of extensive filamentous algal growths, which appeared to lower simuliid and *Aoteapsyche* densities in the unshaded stream.

The effect of the cave on drift differed according to which species was involved. Many were unaffected, although overall the number of taxa, the total drift rate (numbers per unit time) and total drift density were lower at the cave outlet. These differences can be related to the animals drifting capabilities and their ability to survive in the cave on low levels of particulate organic matter. In an earlier study, I found that *Deleatidium* larvae did not drift further inside the cave (travelling about 10 m per drift episode at a current speed of 75 cm s^{-1}) but drifted more often, perhaps in response to low food levels (Death 1988). Animals such as *Deleatidium* sp., *Hydora* sp. (larvae and adults), Simuliidae and Hydrobiosidae that were able to pass the cave successfully, were therefore animals that could both drift well and survive on the little food available in the cave. Animals that apparently did not survive, such as *Olinga feredayi,* although able to eat allochthonous particulate material (Winterbourn 1982) were probably unable to survive long enough given the low food levels and their poor drift ability (McLay 1970).

Why chironomids are unable to survive drifting through the cave is more difficult to explain however, because they feed on fine particulate material (Winterbourn 1982) and many have strong drift capabilities (McLay 1970). Possibly, the frequency with which they enter the drift is lower than by animals like *Deleatidium*, which travel similar distances per drift episode. Most stream chironomids live in tubes, it is therefore unlikely that they will abandon their tubes unless forced to do so, such as during a spate when they may be accidentally dislodged and forced to drift. Support for this idea is gained from the fact that during the spate on 19-20 February, when flow was greater and conceivably drift distances were longer (Elliott 1971), numbers of chironomids were equal in inlet and outlet drift possibly because they were able to travel far enough in a few drift episodes to escape the cave.

Differences in the effect of the cave on drift between the two sampling dates are likely to be related to the spate on 19-20 February which may have increased drift distances as well as washing animals out of the cave, as there are probably few refuges in the cave with the underlying solid limestone.

Despite the cave acting as a barrier to drift for many animals, the communities in the stream above and below the cave were not markedly different from each other in terms of species composition and relative abundance. This indicates the importance of oviposition and perhaps upstream migration from Broken River as the principal modes of colonization for a number of animals in the lower reaches of Cave Stream.

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